

Host Suitability of Nonmaize Agroecosystem Grasses for the Western Corn Rootworm (Coleoptera: Chrysomelidae)

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ABSTRACT The biology of western corn rootworm larvae, *Diabrotica virgifera virgifera* LeConte, on alternate hosts has become an important topic with the recent commercialization of transgenic-rootworm maize. Larval development and survivorship were monitored on 22 plant species, including maize, *Zea mays* L.; maize-field weeds; and selected native prairie grasses, fence-row/forage grasses, and small grain crops planted in greenhouse trials. Small pots containing each plant species were infested with 25 western corn rootworm larvae from a nondiapausing strain. Larval recovery was monitored 7, 14, 21, and 26 d after infestation. The dry weight of larvae and adults was recorded in addition to pronotum width of adults and head capsule width of larvae. Larvae survived at least 14 d on 21 species and 26 d on 18 species. Third instars were recovered from 16 species. The head capsule width of larvae recovered from quackgrass, *Elytrigia repens* L.; Rhodes grass, *Chloris gayana* Kunth; and fall panicum, *Panicum dichotomiflorum* Michx., were not significantly different from maize on all four sample days. Adults were recovered from 10 species. These data along with other studies show that almost all grasses tested provide enough nutrition for larvae of the western corn rootworm to survive 14 d, and larval development to the third instar can occur on most grasses. The potential for rootworm larvae to move between weeds within or adjacent to a maize field could be an important factor in resistance management of transgenic-rootworm maize. However, the long-term implication of such movement for a low-dose transgenic event has yet to be worked out

KEY WORDS *Diabrotica virgifera virgifera*, alternate hosts, resistance management, *Bacillus thuringiensis*, transgenic-rootworm maize.

THE WESTERN CORN ROOTWORM, *Diabrotica virgifera virgifera* LeConte, is a serious pest of maize, *Zea mays* L., especially in fields planted to maize in consecutive years. Feral populations of western corn rootworm have not yet been documented to survive solely on species of plants other than maize. Painter (1951) reported that larvae of the western corn rootworm do not feed on any plants other than maize. However, Branson and Ortman (1967, 1970) observed larval survival to the second instar on 18 of 44 grass species and adult emergence from 12 of 18 grass species. Subsequent research by Clark and Hibbard (2004) has shown that larvae of the western corn rootworm have survived for 24 d on 23 of 28 grass species with adult emergence occurring in five of those species. Oyediran et al. (2004) screened common prairie grass species for western corn rootworm larval host suitability. They recovered adults from 14 of 21 prairie grass species and larvae survived on 20 prairie grass species for at least 10 d. These studies have initiated the

process of identifying other species of plants on which the western corn rootworm could develop.

The importance of understanding the role of alternate hosts in the western corn rootworm life cycle has increased with the commercialization of transgenic maize for rootworm control (EPA 2003) that may be stacked with herbicide resistance. The transgenic maize developed by Monsanto Co. (St. Louis, MO) has been modified to produce an insecticidal protein (Cry3Bb1) from the soil bacterium *Bacillus thuringiensis* Berliner and is offered with herbicide tolerance. Other companies also are developing transgenic maize varieties for rootworm control (Moellenbeck et al. 2001). It has been reported that mortality from larval feeding on the registered event mainly occurs during the first instar (FIFRA Scientific Advisory Panel 2002). This raises the possibility that larvae could begin their development on a grassy weed and then complete its growth on the transgenic plant. It has been reported that Cry3Bb1-expressing maize is not a preferred feeding site when alternatives are available (B.E.H. et al., unpublished data). There also exists the possibility that corn rootworm larvae could taste a transgenic plant and then move to a nearby grassy weed. The use of herbicide-tolerant maize allows farmers to delay weed control, which could increase the possibility of larval movement from weeds

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Table 1. Plant species screened as alternate hosts of western corn rootworm larvae

Species evaluated	Amount planted/pot	Source
Maize (Pioneer Brand 3394)	3 seeds (thinned to 1 plant)	Pioneer Hi-Bred Inc., Johnston, IA
Annual bluegrass	1.0 g	Valley Seed Service, Fresno, CA
Annual ryegrass	1.0 g	Round Butte Seed Growers, Bend, OR
Bermuda grass	2.6 g	Valley Seed Service
Bristle grass	1.5 g	Pogue Agri Partners, Kenedy, TX
Cereal rye	7.0 g	MFA, Columbia, MO
Creeping bentgrass	1.3 g	Round Butte Seed Growers
Dallis grass, <i>Paspalum dilatatum</i> Poirat	5.0 g	Valley Seed Service
Fall panicum	1.5 g	Valley Seed Service
Giant foxtail	3.5 g	Valley Seed Service
Jointed goatgrass, <i>Aegilops cylindrical</i> Host	3.0 g	Valley Seed Service
Kentucky bluegrass	1.0 g	Round Butte Seed Growers
Large crabgrass	2.5 g	Valley Seed Service
Little barley, <i>Hordeum pusillum</i> Nutt	16 whorls	Germplasm Resource Information Network ^a
Purple threeawn, <i>Aristida purpurea</i> Nutt	2.0 g	Native American Seed, Argyle, TX
Quackgrass, <i>Elytrigia repens</i> L.	11.0 g	Valley Seed Service
Rhodes grass	1.5 g	Herbiseed, Twyford, England
Smooth brome	5.0 g	Round Butte Seed Growers
Sorghum	16 seeds	Pioneer Hi-Bred Inc.
Tall fescue	1.8 g	Round Butte Seed Growers
Western wheat grass	20.0 g	Round Butte Seed Growers
Windmillgrass	1.6 g	Dr. Reed Smeda, University of Missouri

^a <http://www.ars-grin.gov/npgs/>.

to maize, and vice versa, because weeds may be present in the maize field longer. These issues raise serious implications for resistance management, which could be negative (Mallet and Porter 1992) or positive. It is fully possible that additional susceptible adults could be produced from within the transgenic field, and if so, would be a positive factor for resistance management.

Farmers who plant transgenic maize are required to follow a resistance management plan, which includes planting a 20% refuge of nontransgenic maize adjacent to or within the transgenic maize field. The refuge is designed to produce rootworms that are susceptible to the Cry3Bb1 protein with the hope that they will mate with any potentially resistant adults emerging from the nearby transgenic maize. An additional supply of beetles not resistant to transgenic maize may be present if larvae are able to survive in a transgenic maize field by partially developing on roots of nearby weeds. However, movement from weeds could enhance the development of resistance to transgenic maize if the progeny of these beetles are more likely to survive transgenic maize. In addition, there could be an increase in the amount of larval injury to transgenic maize if enough larger larvae move to the transgenic maize from weeds.

Oyediran et al. (2004) evaluated prairie grasses as potential hosts from the perspective of attempting to determine the ancestral host (western corn rootworm was first identified from an area without maize). Clark and Hibbard (2004) evaluated a series of grasses, including maize-field weeds. The objective of the current study was to broaden the plant species evaluated for western corn rootworm host suitability to include the remaining maize field grassy weeds not evaluated by Clark and Hibbard (2004) from a resistance management perspective. Western wheat grass, *Agropyron smithii* A. Löve; Rhodes grass, *Chloris gayana* Kunth.;

large crabgrass, *Digitaria sanguinalis* L.; and giant foxtail, *Setaria faberi* Herrm, were identified in previous studies as potential hosts for the western corn rootworm. They are included in this study as controls and to confirm their host suitability.

Materials and Methods

Plant Species and Growing Conditions. The experiment was conducted in the greenhouse during spring 2003. Twenty-two plant species were obtained from several sources and planted in 3.8-liter clay pots containing 2:1 (vol:vol) mixture of autoclaved soil/peat-based growing medium (Promix, Premier Horticulture LTEE, Québec, Canada) (Table 1). The drainage hole of each pot was covered with a fine (114 μ m per opening) stainless steel mesh (TWP Inc., Berkley, CA) to prevent larval escapes. All plants were watered as necessary and provided fertilizer (Peters Professional 20-20-20, Spectrum group, St. Louis, MO) beginning 1 wk after emergence in a greenhouse maintained at 25 \pm 3°C and a photoperiod of 14:10 (L:D) h.

Infestation Procedure. Plant species were in a split-plot arrangement in a randomized complete block design with four replications. For larval recovery, the whole plots of the experiment were plant species and subplots were sample dates. The experimental design for adult recovery was arranged as a randomized complete block with four replications. Five pots of each plant species were required for each replication (one for adult emergence and four for larval sampling times). Pots of the same plant species were randomized and placed adjacent to each other for a given replication. Each set of five pots for each treatment was randomly placed within each replication in the greenhouse. Individual replications were grouped within the greenhouse in a manner that reduced variability within replications (i.e., sunlight and temper-

ature). Five weeks after planting, each pot was infested with 25 healthy neonate western corn rootworm larvae from a nondiapausing colony (Branson 1976) by gently transferring them with a moistened camel's-hair brush from an egg dish to the base of the plant at the soil surface. The nondiapausing colony had been maintained for at least 110 generations (Hibbard et al. 1999). The soil around the plants had been loosened with a small stake to a depth of ≈ 2 cm. Plants were not watered for 24 h after infestation.

Larval and Adult Sampling. Larvae were sampled at 7, 14, 21, and 26 d after infestation. The entire contents of the randomly assigned pots on each day were individually placed in Tullgren funnels equipped with 60-W light bulbs. Collection jars containing water were placed under each funnel and checked up to twice daily for at least 5 d each week. When larvae were observed in the collection jars they were immediately transferred to labeled vials containing 95% ethanol. The number of larvae from each treatment on each of the four sampling dates was recorded. Larval head capsule width was measured using an ocular micrometer (10 \times /21, Wild Co., Heerbrugg, Switzerland) mounted on a microscope (MsZ, Wild Co.). After head capsules were measured, larvae were placed in a desiccating oven (Thelco model 16, GCA/Precision Scientific Co., Chicago, IL) at 90°C for 48 h. Average individual larval dry weights were calculated by weighing all of the larvae from each treatment on each sampling date and dividing by the number of larvae weighed.

On the 26th d after infestation, the plants in the remaining pots for each treatment, except maize, were trimmed to within 3 cm of the soil surface to allow the proper placement of insect mesh (0.60 by 0.60-mm opening; ECONET L, LS Americas Co., Charlotte, NC) over each pot. Trimming the plants to 3 cm killed sorghum, *Sorghum bicolor* L., and cereal rye, *Secale cereale* L., treatments, but the other species continued to grow, and their height was maintained below the mesh. Pots containing maize were covered with insect mesh, but a hole was created in the center of the mesh that was sealed around the stalk of the maize plant with a plastic cable tie. This allowed the maize plant to continue growing while adults were being collected in the mesh. Each pot was checked at least 5 d a week for adults for at least 8 wk after the mesh was placed on the pots and for at least 2 wk after the last adult was collected. All adults were placed in labeled vials containing 95% ethanol. The sex, pronotum width, and dry weight of each adult were recorded in the same manner as for the larvae.

Statistical Analysis. Larval data were analyzed using the MIXED procedure of SAS (SAS Institute 1990). The model contained the main plot of plant species, the subplot of sampling date, replication, and plant species and sampling date interaction. Individual comparisons between plant species within sampling dates and within plant species between sampling dates were conducted for larval data. A separate analysis was done for larval recovery, larval dry weight, and head capsule width. Adult emergence and size were recorded but

not analyzed due to low recovery. The normal probability plot of the residuals of larval recovery, head capsule width, and dry weight indicated that the data were normally distributed and transformations were not necessary.

Results

Larval Recovery. Plant species ($F = 6.53$; $df = 21, 252$; $P < 0.0001$) and sampling date ($F = 3.37$; $df = 3, 9$; $P = 0.0068$) significantly influenced the number of larvae recovered. The plant species and sampling date interaction ($F = 1.50$; $df = 63, 252$; $P = 0.0813$) did not significantly influence the number of larvae recovered, indicating plant species effects were generally consistent over time. Larvae were recovered from all plant species 7 d after infestation and 18 of 22 species 26 d after infestation (Table 2). Larval numbers from maize declined significantly on day 26 because many of the larvae had completed their growth, at least partially accounting for the nearly significant interaction between plant species and sampling date. Fall panicum, *Panicum dichotomiflorum* Michx; large crabgrass; and western wheat grass were the only species whose larval recovery was not significantly different from maize during the first three sample dates. Usually, when larvae were recovered from a plant species, the greatest number of larvae was obtained on days 14 and 21. A notable exception was the relatively large number of larvae recovered from annual bluegrass, *Poa annua* L. (4.50 ± 2.0), on day 7, but significantly fewer larvae were captured on the other three sampling days (Table 2).

Larval Size. Larval head capsule width and dry weight were significantly influenced by plant species ($F = 10.45$; $df = 21, 100$; $P < 0.0001$ and $F = 4.86$; $df = 21, 98$; $P < 0.0001$), sampling date ($F = 55.65$; $df = 3, 9$; $P < 0.0001$ and $F = 32.07$; $df = 3, 9$; $P < 0.0001$), and the plant species and sample date interaction ($F = 1.82$; $df = 54, 100$; $P < 0.0001$ and $F = 1.51$; $df = 52, 98$; $P = 0.0397$) (Table 3). The significant interaction between plant species and sampling date indicates that plant species effects were not constant over time, which makes sense, given that all larvae started out the same size but performed differently on different hosts. The head capsule width of larvae recovered from quackgrass, *Elytrigia repens* L.; Rhodes grass; and fall panicum was not significantly different from larvae captured from maize on all four sample days (Table 3). Seven plant species had larvae with head capsule widths not significantly different from maize based on species main effect (Table 3). Third instars were recovered from 16 of the 22 species evaluated (larval head capsule width of 0.41–0.56 mm) (Hammack et al. 2003). Seven species (maize; fall panicum; quackgrass; smooth brome, *Bromus inermis* Leyss; Rhodes grass; bristle grass, *Setaria geniculata* Beauv; and windmillgrass, *Chloris verticillata* Nutt) produced third instars on day 14. No third instars were recovered from creeping bentgrass, *Agrostis stolonifera* L.; annual ryegrass, *Lolium multiflorum* L.; tall fescue, *Festuca arundinacea* Schreb.; annual bluegrass, or sorghum. Larvae recov-

Table 2. No. western corn rootworm larvae recovered from Tullgren funnels (mean ± SE)

Plant species	Days after infestation				Species main effect
	7	14	21	26	
Western wheat grass	4.25 ± 2.8a-cBC	7.50 ± 1.5aA	7.25 ± 4.4bAB	3.00 ± 2.4a-cC	5.50 ± 1.4a
Fall panicum	3.25 ± 0.6a-dB	5.25 ± 0.9a-cAB	7.50 ± 1.3aA	4.00 ± 0.9aB	5.00 ± 0.6ab
Maize	4.75 ± 1.2aA	6.00 ± 1.4abA	7.25 ± 1.6bA	0.50 ± 0.3deB	4.63 ± 0.9ab
Large crabgrass	1.50 ± 0.5a-dB	4.75 ± 2.6a-dA	4.50 ± 1.2dAB	4.00 ± 0.4abAB	3.69 ± 0.7bc
Giant foxtail	1.75 ± 1.0a-dA	3.25 ± 1.6b-fA	2.75 ± 1.3efA	4.00 ± 1.9aA	2.94 ± 0.7cd
Bermuda grass	3.00 ± 1.2a-dAB	2.50 ± 1.5c-gAB	4.75 ± 1.4cA	1.50 ± 0.3b-dB	2.94 ± 0.6cd
Quackgrass	0.25 ± 0.3dC	5.25 ± 1.2a-cA	3.50 ± 0.6deAB	1.50 ± 0.8b-dBC	2.63 ± 0.6c-e
Purple threeawn	0.25 ± 0.3dB	1.25 ± 1.25efAB	4.25 ± 2.3deA	3.75 ± 3.4abA	2.38 ± 1.1c-e
Rhodes grass	1.00 ± 0.4cdA	1.25 ± 0.8efA	3.50 ± 1.8deA	2.75 ± 1.5a-cA	2.13 ± 0.7d-f
Windmill grass	0.50 ± 0.3dB	4.50 ± 1.8aeA	1.25 ± 1.8efB	2.25 ± 1.3a-cB	2.13 ± 0.6d-f
Cereal rye	2.50 ± 0.3a-dA	0.50 ± 0.3fA	2.50 ± 2.2efA	1.75 ± 0.8bcA	1.81 ± 0.6d-g
Little barley	0.75 ± 0.5dA	2.00 ± 0.7c-fA	2.25 ± 1.1efA	2.00 ± 0.9bcA	1.75 ± 0.4d-g
Annual bluegrass	4.50 ± 2.0abA	1.00 ± 1.0fB	0.25 ± 0.25efB	0.25 ± 0.25eB	1.50 ± 0.8d-g
Bristle grass	0.25 ± 0.3dB	0.50 ± 0.5fB	0.50 ± 0.5efB	3.75 ± 1.0a-cA	1.25 ± 0.6d-g
Creeping bentgrass	1.25 ± 0.6b-dA	1.25 ± 0.9fA	1.75 ± 0.6efA	0.50 ± 0.5c-eA	1.19 ± 0.3e-g
Annual ryegrass	1.75 ± 0.6a-dA	0.50 ± 0.5fA	0.50 ± 0.3efA	0.25 ± 0.25eA	0.75 ± 0.3fg
Jointed goatgrass	0.25 ± 0.3dA	1.50 ± 0.3d-fA	0.75 ± 0.8efA	0.25 ± 0.25eA	0.69 ± 0.2fg
Smooth brome	0.75 ± 0.8dA	1.75 ± 1.8d-fA	0fA	0eA	0.63 ± 0.5fg
Dallis grass	0.75 ± 0.5dA	0.75 ± 0.8fA	0.75 ± 0.5efA	0eA	0.56 ± 0.2fg
Tall fescue	1.25 ± 0.9b-dA	0fA	0fA	0eA	0.31 ± 0.3g
Kentucky bluegrass	0.25 ± 0.3dA	0.50 ± 0.5fA	0fA	0.25 ± 0.25eA	0.25 ± 0.1g
Sorghum	0.75 ± 0.5dA	0.25 ± 0.25fA	0fA	0eA	0.25 ± 0.1g
Sampling day main effect	1.61 ± 0.2B	2.36 ± 0.3AB	2.53 ± 0.4A	1.64 ± 0.3B	

Significant differences ($P \leq 0.05$) between plant species within a column are indicated by different lowercase letters. Significant differences between sample dates within plant species are indicated by different uppercase letters.

ered from 12 plant species had significant intraspecific weight gains (Table 4). Larvae recovered from maize were significantly heavier than larvae from all other plant species on days 21 and 26 and in overall larval weight.

Adult Recovery and Size. At least one adult was recovered from 10 of the plant species. However, adult recovery was minimal with a total of 11 adults (six female, five male) recovered from maize and nine adults (eight female, one male) from Bermuda grass,

Table 3. Average head capsule widths (millimeters) of larvae captured from each host species (mean ± SE)

Plant species	Days after infestation				Species main effect
	7	14	21	26	
Quackgrass	0.35 ± 0.07aB	0.49 ± 0.02aA	0.54 ± 0.02aA	0.51 ± 0.03aA	0.507 ± 0.02a
Purple threeawn	0.30 ± 0.07a-cC	0.42 ± 0.04bcBC	0.50 ± 0.03a-cAB	0.52 ± 0.03aA	0.495 ± 0.02a
Bristle grass	0.20 ± 0.07cC	0.45 ± 0.05abB	0.40 ± 0.05c-fB	0.53 ± 0.02aA	0.493 ± 0.03ab
Maize	0.37 ± 0.02aB	0.52 ± 0.02aA	0.53 ± 0.02aA	0.55 ± 0.05aA	0.488 ± 0.01ab
Fall panicum	0.33 ± 0.02aB	0.50 ± 0.02aA	0.52 ± 0.02aA	0.51 ± 0.02aA	0.482 ± 0.01ab
Rhodes grass	0.33 ± 0.04abB	0.46 ± 0.04aA	0.50 ± 0.03acA	0.54 ± 0.03aA	0.481 ± 0.02a-c
Large crabgrass	0.35 ± 0.03aB	0.39 ± 0.02bcB	0.55 ± 0.02aA	0.53 ± 0.02aA	0.470 ± 0.01a-c
Windmill grass	0.25 ± 0.05a-cC	0.43 ± 0.02bcB	0.47 ± 0.04adAB	0.52 ± 0.03aA	0.451 ± 0.02b-d
Little barley	0.35 ± 0.04aB	0.38 0.03bcB	0.44 ± 0.03b-eB	0.55 ± 0.03aA	0.446 ± 0.02cd
Western wheat grass	0.33 ± 0.03aB	0.39 ± 0.02bcB	0.52 ± 0.02aA	0.52 ± 0.03aA	0.441 ± 0.01d
Cereal rye	0.30 ± 0.02a-cB	0.33 ± 0.05c-eB	0.51 ± 0.03abA	0.49 ± 0.03aA	0.417 ± 0.02de
Bermuda grass	0.26 ± 0.02a-cC	0.34 ± 0.03b-eC	0.45 ± 0.02b-dB	0.54 ± 0.03aA	0.389 ± 0.01ef
Smooth brome	0.23 ± 0.04cB	0.47 ± 0.04aA			0.382 ± 0.04ef
Jointed goatgrass	0.40 ± 0.07aA	0.36 ± 0.03b-dA	0.37 ± 0.05d-fA	0.50 ± 0.07aA	0.377 ± 0.03ef
Giant foxtail	0.24 ± 0.03bcB	0.33 ± 0.03c-eB	0.35 ± 0.03efAB	0.40 ± 0.02bA	0.346 ± 0.01f
Kentucky bluegrass	0.35 ± 0.07aA	0.33 ± 0.05c-eA		0.30 ± 0.07cA	0.325 ± 0.01fg
Dallis grass	0.20 ± 0.04cB	0.27 ± 0.05deB	0.45 ± 0.04b-eA		0.306 ± 0.04fg
Annual ryegrass	0.25 ± 0.03a-cA	0.35 ± 0.05b-eA	0.35 ± 0.05efA	0.35 ± 0.07bcA	0.292 ± 0.03g
Creeping bentgrass	0.27 ± 0.03a-cA	0.28 ± 0.04deA	0.32 ± 0.03fA	0.30 ± 0.05cA	0.292 ± 0.02g
Sorghum	0.20 ± 0.07cA	0.30 ± 0.07c-eA			0.250 ± 0.05gh
Tall fescue	0.24 ± 0.04bc				0.240 ± 0.04gh
Annual bluegrass	0.23 ± 0.02cA	0.21 ± 0.04eA	0.30 ± 0.07fA	0.35 ± 0.07bcA	0.231 ± 0.03h
Sampling day main effect	0.29 ± 0.01C	0.41 ± 0.01B	0.49 ± 0.01A	0.50 ± 0.01A	

First instar, 0.20–0.26 mm; second instar, 0.27–0.40; third instar, 0.41–0.56. Significant differences ($P \leq 0.05$) between plant species within a column are indicated by different lowercase letters. Significant differences between sample dates within plant species are indicated by different uppercase letters.

Table 4. Average dry weight (milligrams) of larvae captured from each host species (mean \pm SE)

Plant species	Days after infestation				Species main effect
	7	14	21	26	
Maize	0.153 \pm 0.018aC	0.450 \pm 0.019aC	1.085 \pm 0.069aA	1.640 \pm 0.120aB	0.656 \pm 0.057a
Quackgrass	0.080bC	0.466 \pm 0.035aBC	0.709 \pm 0.049bcAB	1.155 \pm 0.101bA	0.636 \pm 0.047b
Little barley	0.153 \pm 0.003aB	0.140 \pm 0.015abB	0.448 \pm 0.122b-dB	1.198 \pm 0.135bA	0.557 \pm 0.071bc
Fall panicum	0.150 \pm 0.019aC	0.390 \pm 0.028abBC	0.847 \pm 0.063bA	0.554 \pm 0.023cdAB	0.552 \pm 0.038bc
Purple threeawn	0.130abB	0.410 \pm 0.0abAB	0.506 \pm 0.110b-dAB	0.577 \pm 0.017cdA	0.512 \pm 0.049bc
Rhodes grass	0.130 \pm 0.016abB	0.278 \pm 0.005abAB	0.568 \pm 0.020b-dA	0.611 \pm 0.034cdA	0.488 \pm 0.033bc
Large crabgrass	0.133 \pm 0.008abB	0.204 \pm 0.011abB	0.548 \pm 0.056b-dA	0.856 \pm 0.072bcA	0.481 \pm 0.044bc
Bristle grass	0.050bB	0.070 \pm 0.0abAB	0.130 \pm 0.0dAB	0.549 \pm 0.072cdA	0.434 \pm 0.070cd
Cereal rye	0.110 \pm 0.013bB	0.225 \pm 0.025abAB	0.588 \pm 0.032b-dAB	0.486 \pm 0.136cdA	0.373 \pm 0.052cd
Windmill grass	0.100 \pm 0.020bB	0.282 \pm 0.029abB	0.462 \pm 0.118b-dAB	0.560 \pm 0.095cdA	0.371 \pm 0.041cd
Bermuda grass	0.041 \pm 0.005bB	0.160 \pm 0.008abB	0.220 \pm 0.008dB	0.955 \pm 0.178bA	0.255 \pm 0.046cd
Western wheat grass	0.068 \pm 0.001bB	0.199 \pm 0.009abB	0.270 \pm 0.010cdAB	0.399 \pm 0.067cdA	0.228 \pm 0.015cd
Smooth brome	0.110 \pm 0.06bA	0.260 \pm 0.003abA			0.215 \pm 0.023cd
Jointed goatgrass		0.117 \pm 0.006abA	0.190 \pm 0.0dA	0.400cdA	0.167 \pm 0.028d
Giant foxtail	0.129 \pm 0.018abA	0.106 \pm 0.004abA	0.175 \pm 0.009dA	0.203 \pm 0.030dA	0.157 \pm 0.013d
Sorghum	0.110bA	0.200abA			0.155 \pm 0.045d
Dallis grass	0.060 \pm 0.0bA	0.040 \pm 0.0abA	0.347 \pm 0.053cdA		0.149 \pm 0.052d
Creeping bentgrass	0.058 \pm 0.021bA	0.036 \pm 0.007bA	0.203 \pm 0.068dA	0.050 \pm 0.0dA	0.102 \pm 0.030d
Annual ryegrass	0.057 \pm 0.002bA	0.020 \pm 0.0bA	0.155 \pm 0.005dA	0.320dA	0.089 \pm 0.024d
Kentuckybluegrass		0.090 \pm 0.0abA		0.070dA	0.083 \pm 0.007d
Tall fescue	0.080 \pm 0.010b				0.080 \pm 0.011d
Annual bluegrass	0.055 \pm 0.003bA	0.060 \pm 0.0abA	0.220dA	0.360cdA	0.075 \pm 0.014d
Sampling day main effect	0.097 \pm 0.005C	0.266 \pm 0.011B	0.55 \pm 0.026A	0.615 \pm 0.031A	

Significant differences ($P \leq 0.05$) between plant species within a column are indicated by different lowercase letters. Significant differences between sample dates within plant species are indicated by different uppercase letters.

Cynodon dactylon L. (Table 5). Four or fewer adults were recovered from each of the remaining eight plant species. Females recovered from maize were heavier (3.08 ± 1.53 mg) than females recovered from the other plant species ($0.82\text{--}2.10$ mg) (Table 5). Females from maize generally had larger pronotum widths than females from the other treatments with the exception of females from sorghum and quackgrass (Table 5).

Discussion

The combination of transgenic maize for rootworm control with herbicide tolerance may create a situation where larvae are exposed to a selection pressure in the presence of alternate food sources, because

farmers can delay weed control. The ramifications of this event are unclear, but it could be positive or negative from a resistance management perspective. Because western corn rootworm larvae survived at least 14 d on 21 of 22 grass species evaluated and developed to at least the second instar on 18 of 22 species, initial development on a grassy-maize-field weed followed by movement to a transgenic maize plant when the weed is removed with herbicide application might well be a common occurrence. If so, one scenario would be that beetles produced in the transgenic field may be of a susceptible genotype and could add to the pool of susceptible beetles from the refuge. These beetles also would be in proximity to any potential resistant beetles emerging from the trans-

Table 5. Total no. adults captured from each species, no. each sex, their average dry weight (milligrams), and pronotum width (millimeters) (mean \pm SE)

Plant species	No. adults	Female adults			Male adults		
		No.	Dry weight	Pronotum width	No.	Dry weight	Pronotum width
Maize	11	6	3.08 \pm 1.53	1.57 \pm 0.05	5	1.20 \pm 0.07	1.36 \pm 0.02
Bermuda grass	9	8	0.82 \pm 0.09	1.21 \pm 0.03	1	0.56	1.25
Large crab	4	2	0.90 \pm 0.14	1.30 \pm 0.15	2	1.23 \pm 0.18	1.23 \pm 0.08
Western wheat	3	2	2.10 \pm 1.22	1.40 \pm 0.10	1	0.75	1.25
Rhodes grass	2	2	0.95 \pm 0.20	1.03 \pm 0.08	0		
Sorghum	2	1	1.6	1.45	1	1.47	1.25
Fall panicum	1	0			1	1.01	1.20
Little barley	1	0			1	1.24	1.20
Quack grass	1	1	1.61	1.55	0		
Cereal rye	1 ^a						

No adults were recovered from plant species not listed.
^a Adult escaped before sex, weight, or pronotum width could be determined.

genic maize. A second and less desirable scenario would be that the exposure to transgenic maize could lead to resistance in the progeny of these individuals.

In the current study, three species (western wheat grass, large crabgrass, and fall panicum) consistently produced a similar number of larvae as maize over the four sampling dates. Large crabgrass and fall panicum are summer annuals that are common in maize fields throughout the United States. The timing of germination and significant root availability of these two species are more likely to overlap with late hatching larvae and/or second and third instars in many areas. Depending on the geographic region and seasonal conditions, there may be more or less overlap of neonate larvae and the roots of these species. Clark and Hibbard (2004) identified western wheat grass as a potential host of western corn rootworm. Western wheat grass is a cool-season forage crop commonly grown in areas requiring drought-tolerant qualities. Our data confirm results of Clark and Hibbard (2004) that western wheat grass is capable of sustaining larval development. However, the simultaneous occurrence of western wheat grass and maize within proximity of each other is unlikely. Because western wheat grass is present during the spring when larval development is occurring, it could be a host if eggs were laid in proximity the previous year.

Larval recovery from quackgrass (2.63 ± 0.6) was about one-half of that observed in maize (4.63 ± 0.9). However, the larval weight and head capsule width were not significantly different from larvae collected from maize. Quackgrass is a perennial early season grass that is present in maize fields during the early growing season when larval development is occurring.

Bermuda grass is a warm-season perennial that reproduces by seeds, rhizomes, and stolons. It is considered a weed of field crops and lawns, but it also is used as a turfgrass. Nine adults were recovered from Bermuda grass, second only to maize (11). Overall larval weight was low for Bermuda grass, but significant larval growth was observed on sampling day 26. Bermuda grass could potentially be a host of western corn rootworm based on the data reported here, and its temporal overlap with western corn rootworm larvae in and around maize fields.

Our results agree with those of Clark and Hibbard (2004) that Rhodes grass does sustain larval development. Rhodes grass is a perennial forage crop cultivated in dry regions, which may limit its overlap with the distribution of western corn rootworms.

We evaluated five species that were in common with species evaluated by Branson and Ortman (1967, 1970): western wheat grass; Kentucky blue grass, *Poa pratensis* L.; cereal rye; smooth brome; and sorghum. We are in agreement that western wheat grass is a host for western corn rootworm and that Kentucky bluegrass and sorghum are poor or nonhosts. However, two adults were recovered from sorghum in our study, even though no larvae were recovered on days 21 and 26. Sorghum is likely a nonhost of western corn rootworm based on larval size in this study and evaluations of sorghum in Clark and Hibbard (2004) and Oyediran

et al. (2004). Our study, based on larval recovery, indicates that smooth brome and cereal rye are poor hosts for the western corn rootworm. Branson and Ortman (1970) reported that smooth brome was a nonhost with no larval survival after 10 d. Differences between these two studies could be procedural (petri dishes versus greenhouse pots).

Higher adult emergence was expected from maize. In total, 200 larvae were infested on maize plants across all replications, and only 11 adults (5.5%) were recovered. These numbers are lower than Oyediran et al. (2004) (30%) but similar to Clark et al. (2004) (4.5%), both of whom used similar materials and methods to our experiment. It is not clear why adult emergence is low.

Our data suggest that western corn rootworm larval development could occur on almost all nonmaize grass plant species tested. However, it is unknown whether larvae of the western corn rootworm are currently using other plant species for development or whether this is just a potential food source. It is likely that the future use and toxicity of transgenic maize for rootworm control will increase. If so, it is a possibility that the western corn rootworm will adapt to use other plant species. The western corn rootworm has already demonstrated the ability to lose its preference for laying eggs in maize in a response to the widespread practice of crop rotation (Levine and Gray 1996, Levine et al. 2002, O'Neal et al. 1999). This may be the first step to the western corn rootworm adapting to other plant species for larval development (Clark and Hibbard 2004).

More research needs to be conducted to determine specifically how beetles fully or partially surviving on nonmaize hosts will impact a resistance management program. Currently, no studies have shown that larvae are surviving on weeds in or near actual maize fields. However, this is a difficult event to document and, if occurring, may not be widespread at this time.

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